COMPETITION MODELS

BU-175-M   Keewhan Choi   February, 1965

ABSTRACT

In this paper several deterministic models for competition between two species proposed by Bartlett, Kendall, Lotka and Volterra are reviewed. First two simple models are discussed in detail to study the behavior of two species near the equilibrium point.

Simple models are then modified to take into consideration such quantities as maturation lag and immigration.

In the last part, a general competition model is discussed briefly. Also the work on flowerbeetle by Park is reviewed.

The material in pages 12 through 23 are excerpts from the 1962 lecture notes (unpublished) of S. Karlin.

Prey-Predator Models

1.1. The problem we will consider deals with two species, the first of which serves as food for the second one. Let

H(t) be the size of the host population at time t

P(t) be the size of the parasite population at time t

β be the birth rate of the host population; βdt is the increase in the population per single host organism in the time interval dt

δ be the death rate of the parasite population .

We shall assume that the number of kills of host by parasites at time t is proportional to H(t)P(t).

The differential equations giving the rate of change in population sizes are:

(I)

$$\frac{dH}{dt} = \beta H(t) - \gamma_1 P(t)H(t)$$

$$\frac{dP}{dt} = \gamma_2 P(t)H(t) - \delta P(t) \ , \quad \beta, \ \gamma_1, \ \gamma_2, \ \delta > 0$$

(Note that γ_1 can be interpreted as the probability of contact between a host organism and a parasite and γ_2 the fraction of parasites which survive to maturity.)

Models of this general type have much wider applicability. To mention but one example that is quite different from prey-predator, consider the spread of a fatal disease by means of bacteria. We can take the human population of the region as H(t), and the bacteria as P(t).

It will be interesting to consider a second model, similar in form, but leading to quite different solutions. Suppose that we consider two species of hunters (x(t), y(t)) that are in competition with each other, so that members

of one species kill members of the other species. Each one has a natural rate of increase in the absence of its enemy, with expansion rates with parameters a, c. Each species decreases proportionally to the product xy as a result of kills by the other species. Hence the simplest model is given by

$$\text{(II)} \qquad \frac{dx}{dt} = ax - bxy \; ; \quad \frac{dy}{dt} = cy - dxy \; , \quad a, b, c > 0 \; .$$

1.2. The differential equations

The equations of the model in Section 1 are examples of a particularly interesting type of simultaneous first order differential equations. They are of the form:

$$\text{(*1)} \qquad \frac{dH}{dt} = F(H, P) \; ; \quad \frac{dP}{dt} = G(H, P) \; .$$

These equations have the special property that time does not enter them explicitly. As a matter of fact, time can be eliminated by dividing the second equation by the first:

$$\text{(*2)} \qquad \frac{dP}{dH} = \frac{G(H, P)}{F(H, P)}$$

Often, we are interested only in the possible values of the quantities P and H, which we shall represent geometrically by the position of the points (H, P). As we do not care to know the exact times when these positions are occupied the above equation (*2) gives all interesting information. The locus of the position through time, known as the trajectory, must be a solution of the first order differential equation (*2).

Such equations have been studied extensively. We shall summarize only a few of the known results.

Theorem 1. · If (H_o, P_o) is a point of the plane near which the partial derivatives of F and G are continuous, then there is a unique solution of (*1) passing through (H_o, P_o), at t = 0. The solutions are either constant functions of time, or they describe a simple curve. Furthermore, the solutions H(t) and P(t) depend continuously on the initial position.

We can draw many useful conclusions from the theorem.

We note that in our case the trajectories do not depend on the starting time. Thus if $H(t_o) = H_o$, $P(t_o) = P_o$ at a certain time t_o, then for any time

after t_o the trajectories are as if the process at time 0 started at (H_o, P_o); i.e., $H(t - t_o)$ and $P(t - t_o)$ agree with the function $H'(t)$ and $P'(t)$ which one would have if $H(o) = H_o$, $P(o) = P_o$. Hence, there is a unique trajectory through each point. An immediate consequence is that two trajectories cannot cross, for we would then have two different trajectories through the same point. A trajectory also cannot cross itself, since by (*1) the direction of motion depends only on the position, not on the time. The trajectories given by theorem 1 are, of course, solutions of (*2).

We must now discuss solutions that are constant functions of time. These occur at equilibrium points; i.e., points where $F = G = 0$. If we choose such a point as the starting position, then the rate of changes in (*1) are 0, and so we remain at the starting point. We thus have a one-point trajectory.

If the starting point is not an equilibrium point, then the trajectory is a simple curve. Furthermore, this curve must be traversed in a fixed direction, since (*1) determines the direction of motion for every point of the trajectory. This direction could be reversed only if we reached an equilibrium point, or if the curve crossed itself, which is impossible. However, an equilibrium point cannot lie on a curve trajectory: If it did, the curve trajectory would have a point in common with the point trajectory, and we would have two trajectories through the same point. Thus, an equilibrium point can never be reached if we start out of equilibrium. But this does not prevent the trajectory from approaching the equilibrium point asymptotically. That is, the position gets closer and closer to the equilibrium position, although it never reaches it in finite time. The equilibrium is the limit of the position as $t \to \infty$.

It is of particular interest to know how a trajectory behaves in the neighborhood of an equilibrium point. We shall illustrate three kinds of behavior: (1) Whenever we start near the equilibrium. This is known as a stable equilibrium point. (2) Whenever we start near the equilibrium, we proceed away from it; such an equilibrium is known as unstable. (3) Whenever the trajectory is a closed curve with the equilibrium point on the inside, we move cyclically around the equilibrium.

A major tool in determining the nature of the behavior is given in the following theorem.

Theorem 2. The nature of a trajectory near an equilibrium point may be determined by expanding F and G in a Taylor series around the equilibrium, and keeping only one linear term. The solutions of these linear equations near the equilibrium will have the same general nature as the exact solution.

> We have considered only two equations in two unknowns. But the discussion just concluded holds equally well when there are n equations in n unknowns:
>
> $$(*1)' \qquad \frac{dx_i}{dt} = F_i(x_1,\ldots,x_n)$$
>
> for $i = 1,\ldots,n$.

1.3. Solution of the equations

At first we will concentrate on the model generated by the equations in (I). We shall be interested only in trajectories in the first quadrant. Our first task will be to show that if $H_o > 0$ and $P_o > 0$, then $H(t) > 0$ and $P(t) > 0$ for all t.

Let us start by discussing four special trajectories. First, there are only two equilibrium points $(0, 0)$ and $E = (\delta/\gamma_2, \beta/\gamma_1)$. Thus we have two one-point trajectories. But the positive parts of the axes are also trajectories. Since trajectories cannot cross, a trajectory starting inside the first quadrant can never cross either axis, and hence $H(t) > 0$ and $P(t) > 0$ for all time.

The interesting equilibrium point is E. Let us find the nature of the trajectories near E. Let $u = H - \delta/\gamma_2$ and $v = P - \beta/\gamma_1$. Then

$$\frac{du}{dt} = \frac{dH}{dt} = -(u + \delta/\gamma_2)\gamma_1 v \; ; \text{ and } \frac{dv}{dt} = \frac{dP}{dt} = \gamma_2 u(v + \beta/\gamma_1) \; .$$ The linear part of these equations are.

$$(*3) \qquad \frac{du}{dt} \approx - \frac{\gamma_1 \delta}{\gamma_2} v$$

$$\frac{dv}{dt} \approx \frac{\beta \gamma_2}{\gamma_1} u$$

Treating these as exact equations in accord with Theorem 2, differentiating the first equation, and substituting $\frac{dv}{dt}$ from the second, we get

(*4)
$$\frac{d^2u}{dt^2} = -\beta\delta u \ .$$

The motion will therefore be periodic. Since the starting time is unimportant, let us start at a time when u = 0. The solution of (*4) is then

$$u = A \sin (\sqrt{\beta\delta}t)$$

and from (*3) we obtain a solution of the form

$$v = B \cos (\sqrt{\beta\delta}t) \ .$$

Thus

$$\frac{u^2}{A^2} + \frac{v^2}{B^2} = 1 \ .$$

Hence, the trajectory is an ellipse.

We have thus shown that near E the trajectories must be closed, and hence that solutions are periodic movements around the equilibrium point. In first approximation the trajectories are elliptical, and the period of revolution is $2\pi/\sqrt{\beta\delta}$.

To find the trajectories exactly, we form the equation corresponding to (*2).

(*5)
$$\frac{dP}{dH} = \frac{P(\gamma_2 H - \delta)}{H(\beta - \gamma_1 P)}$$

Hence
$$\frac{\beta - \gamma_1 P}{P} \ \frac{dP}{dH} + \frac{\delta - \gamma_2 H}{H} = 0 \ .$$

Integrating with respect to H, we obtain

$$\beta \log P - \gamma_1 P + \delta \log H - \gamma_2 H = \log K$$

or

(*6)
$$\frac{H^\delta}{e^{\gamma_2 H}} \cdot \frac{P^\beta}{e^{\gamma_1 P}} = K$$

Since K does not depend on time,

$$K = \frac{H_0^\delta}{e^{\gamma_2 H_0}} \ \frac{P_0^\beta}{e^{\gamma_1 P_0}} \ .$$

We have thus found an equation for the trajectory corresponding to a given starting position. The function $H^\delta / e^{\gamma_2 H}$, or the like function $P^\beta / e^{\gamma_1 P}$ has a graph similar to Figure 1, and so each possible value is taken on twice, except for the extreme values.
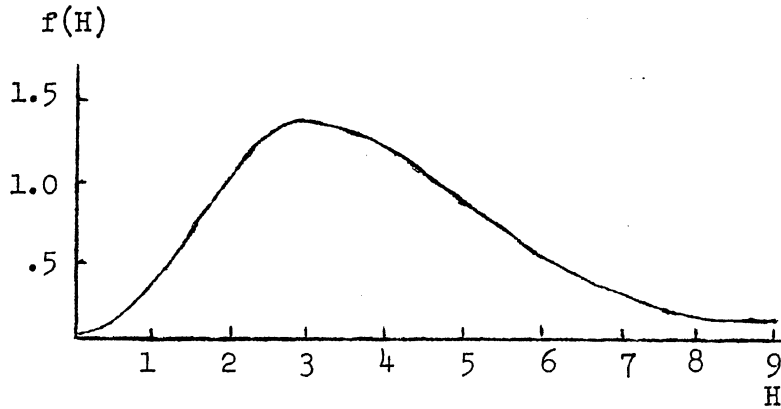

Figure 1. $f(H) = \dfrac{H^\delta}{e^{\gamma_2 H}}$ for $\gamma_2 = 1$, $\delta = 3$

Thus if in (*6) we fix H at a possible value, there are normally two corresponding P-values, and for a possible P-value there are normally two possible H-values. Thus we obtain a simple closed curve. The maximum and minimum P-values are taken on for $H = \delta/\gamma_2$, while the maximum and minimum H-values occur for $P = \beta/\gamma_1$, and there are no inflection points. A family of such trajectories is shown in Figure 2.
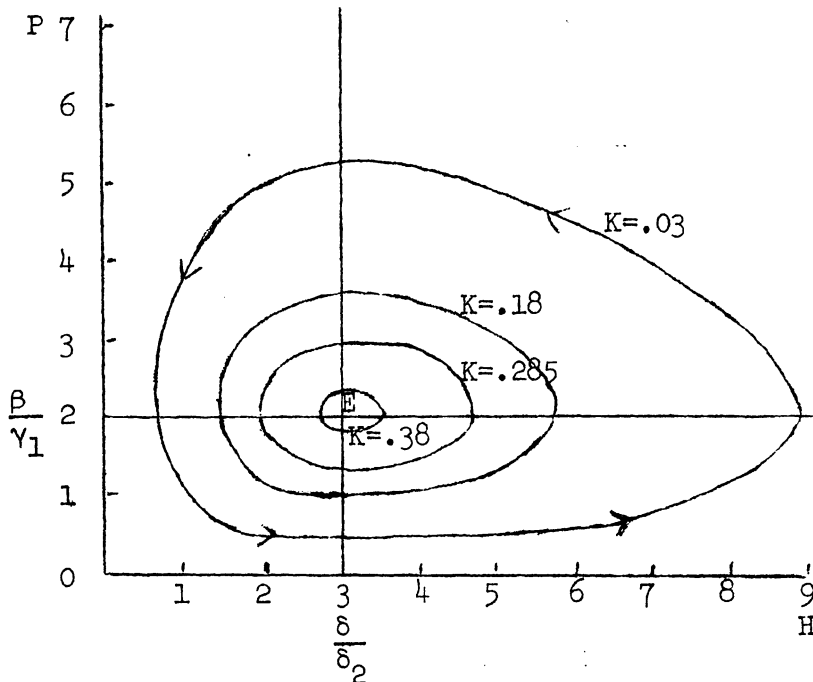

Figure 2. Trajectories $\dfrac{H^\delta}{e^{\gamma_2 H}} \cdot \dfrac{P^\beta}{e^{\gamma_1 P}} = K$ for $\beta = 4$, $\gamma_1 = 2$, $\gamma_2 = 1$, $\delta = 3$

We must still determine the direction of motion. From (I), $\frac{dH}{dt} > 0$ if and only if $P < \beta/\gamma_1$. Hence, on the lower half of the trajectory H is increasing, whereas on the upper it is decreasing. Therefore, the motion must be clockwise.

As a final result we shall obtain the average values $\bar{H}$ and $\bar{P}$. Since the motion is cyclic, we may take the average over one cycle. Let T be the length of a cycle. From (I),

$$\frac{1}{H} \frac{dH}{dt} = \beta - \gamma_1 P$$

$$\int_0^T \frac{1}{H} \frac{dH}{dt}\, dt = \int_0^T (\beta - \gamma_1 P)dt$$

(*7)
$$\log (H(T)) - \log (H(o)) = \beta T - \gamma_1 \int_0^T Pdt$$

$$= T[\beta - \gamma_1 \bar{P}] \ .$$

But (0, T) is a complete cycle; hence $H(o) = H(T)$. Thus the lefthand side of (*7) is 0, and hence so is the righthand side. Thus $\bar{P} = \beta/\gamma_1$. And similarly, $\bar{H} = \delta/\gamma_2$. These averages turn out to be independent of the initial position and hence are the same as the equilibrium values at E.

Let us now turn to the second model, which is generated by the equations in (II). We find the same equilibrium points as before, and the axes are again special trajectories. Thus a trajectory starting with positive values for x and y will continue to have positive values. The major difference arises when we find the behavior near E. By the approximation used in (*3), we find

(*3)'
$$\frac{du}{dt} = - \left(\frac{bd}{c}\right) v$$

$$\frac{dv}{dt} = - \left(\frac{ac}{b}\right) u \ .$$

And thus,

(*4)'
$$\frac{d^2u}{dt^2} = adu \ .$$

In this case the solution is _not_ periodic. The most general solution of this equation is $u = Ae^{st} + Be^{-st}$, where $s = \sqrt{ad}$. If we differentiate this and substitute the result in $(*3)'$, we obtain $v = - rAe^{st} + rBe^{-st}$, in which $r = cs/bd$. From these solutions we find the relation $u^2 - (v/r)^2 = 4AB$; hence, the first approximation trajectories are hyperbolas, with E as center.

Therefore, we know that the motion is not periodic, and the trajectories approach the equilibrium point for a while - and then run away from it. To obtain more information concerning the trajectories we carry out the method of Equations $(*5)$ and $(*6)$ to find

$$(*5)' \qquad \frac{dy}{dx} = \frac{y(d - cx)}{x(a - by)}$$

and $(*6)'$
$$\frac{y^a}{e^{by}} = K \frac{x^d}{e^{cx}} \; ; \quad K = \frac{y_0^a \, e^{cx_0}}{e^{by_0} x_0^d}$$

Particularly interesting are the curves passing through E, i.e., where

$$K = \frac{(\frac{a}{b})^a \, e^{c(d/c)}}{e^{b(a/b)} \, (\frac{d}{c})^d} = (\frac{a}{b})^a (\frac{c}{d})^d e^{d-a}$$

These are shown by solid lines in Figure 3. Since trajectories cannot cross, and since E is a point trajectory, the remainder of these curves must actually represent four separate trajectories. By considering the signs of the derivatives in $(*3)'$, we see that two of these correspond to asymptotic approach to the equilibrium E whereas two represent asymptotic regress from the equilibrium. These curves divide the positive quadrant into four regions. If the process starts in a given region it must stay there. The shape of a trajectory and the direction of motion is then determined by the signs of $\frac{dy}{dx}$ and $\frac{d^2y}{dx^2}$. Representative examples are shown in Figure 3.

There is, of course, no analogue to (11), since the motion is not periodic.
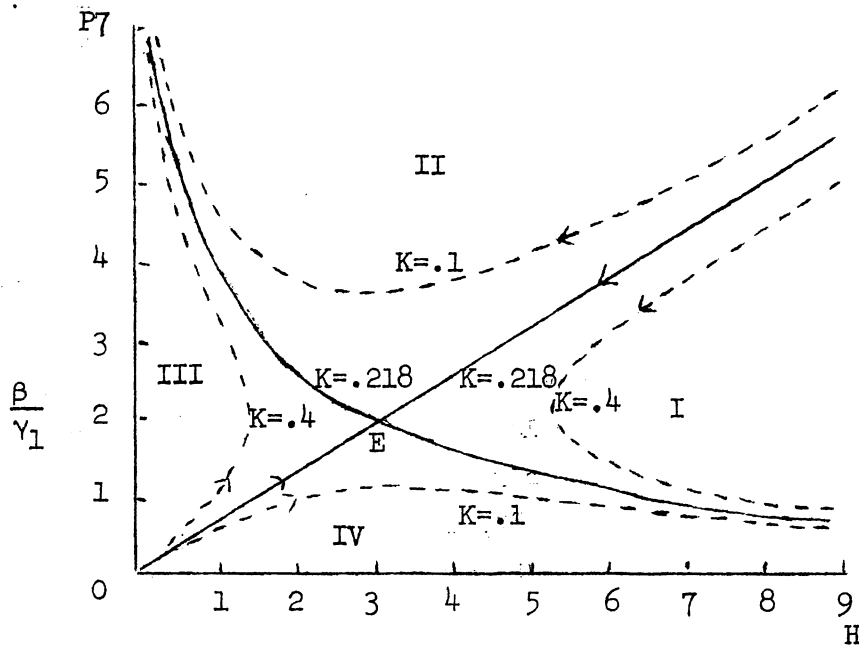
Figure 3 Trajectories $\dfrac{y^a}{e^{by}} = K \dfrac{x^d}{e^{cx}}$ $a = 4$, $b = 2$
     $c = 1$, $d = 3$

1.4. Interpretation of the results

In the model for (I) we have cyclic behavior. Our cycle always starts with a positive number of hosts and parasites. It is extremely unlikely that we should start exactly with the equilibrium values; hence, we may assume that we shall follow a closed curve trajectory, as in Figure 2. We shall therefore observa a cyclic process of four stages: (I) Hosts are in abundance. The number of parasites increases, cutting down on the number of hosts. (II) When the hosts drop to $H = \delta/\gamma_2$, the parasites find insufficient food and hence start declining in number. Hosts continue to decline. (III) When parasites drop to $P = \beta/\gamma_1$ in number, hosts can start increasing in number. Parasites continue to decline. (IV) When hosts get back up to $H = \delta/\gamma_2$, parasites start increasing again, until they reach a level of $P = \beta/\gamma_1$. At this point stage I is reentered. The fact that the trajectories can never reach an axis means that neither species will ever be wiped out. Thus, we have a type of cyclic equilibrium.

The average number of hosts is δ/γ_2, and of parasites β/γ_1, independently of the starting stocks. Thus, the equilibrium values are determined by the

machinery of change, given by (I), and not by the starting values. The
starting values influence only how widely the values vary. The further we
start from equilibrium, the wider the variation.

Figure 2 shows four closed trajectories for the case $\beta = 4$, $\gamma_1 = 2$,
$\gamma_2 = 1$, $\delta = 3$. The equilibrium point is E = (3,2). The curves, from the
inside out, correspond to starting positions (3, 1.75); (3, 1.3); (3,1) and
(3,5). (The trajectories were traced out by numerical approximation on a
computing machine.

It is seen that the innermost trajectory is very near an ellipse, whereas
the ones further out become more lopsided. Our first approximation solution
for the length of the cycle yields $T = 2\pi/\sqrt{\beta\delta} = 1.814$. The numerical esti-
mates of the trajectories yield 1.87, 1.84, 1.88, and 2.04, respectively.
Thus the approximation is excellent near E, and it is fairly good even further
out. Thus, although the sizes of the species vary greatly according to the
initial stocks, the times of revolution changes very little for reasonable
values.

In the model for (II) we note that the normal asymptotic behavior is one
of approaching an axis. That is, although no species die out in finite time,
one tends to vanish asymptotically. If we take into account that there cannot
be less than one animal per species, this really amounts to the prediction of
the eventual extinction of one species. The other species, on the other hand,
tends to infinity. Of course this too is an oversimplification, in that the
model neglects shortage of the food supply.

There are again four important regions, but this time they determine the
long-range outcome: (I) They are large number of both species to start with.
This causes a steady decrease in both species (because of the large number of
kills), until the second species drops to the critical level of $y = a/b$. Then
the first species start to increase again and is able to wipe its enemy out.
(II) This is like I, except that the critical level is $x = d/c$, and it is the
first species that is eliminated. (III) There are small numbers to start
with, and hence very little conflict. Thus each species can increase, until
the second species reaches the critical level of $y = a/b$. Then it begins to
dominate the first species, and eventually eliminates it. (IV) This is like
III, except for the fact that the critical level is $x = d/c$, and it is the

second species that die out.

The exceptions to these rules occur on the boundaries of the regions, which consist of the four special trajectories marked solidly in Figure 3, and of the point E itself. The boundary of I and IV shares with both regions the feature that the second species is wiped out, but the increase in the first species and the decrease in the second both take place monotonically. The boundary of II and III is similar, with the first species being wiped out. But if the initial numbers of the two species happen to fall on the border of I and II, or of III and IV, then the numbers tend to the equilibrium value E monotonically. At E itself no change can take place. Of course, any such starting combination is very unlikely.

Competition models II

Unfortunately, the two models we have considered fail to fit observed situations well. We shall consider several modifications which are more sophisticated.

First, we shall consider a case of one species and examine the growth of the population of mature members.

Let $\qquad$ $N(t)$ = size of population of mature individuals at time t

$\qquad$ τ $\quad$ = time to grow to maturity

$\qquad$ α $\quad$ = birth rate

$\qquad\qquad$ (ignore the death rate)

Then

$$\frac{dN}{dt} = \alpha N(t - \tau)$$

This equation has solutions which may be prescribed arbitrarily for $0 \leq t \leq \tau$. We found in the last lecture, that if time to develop to maturity was not considered, the population size approached e^{mt} where m is the Mathusian constant. Let us try a solution of that form. It must satisfy $m e^{mt} = \alpha e^{mt} e^{-m\tau}$ so $m = \alpha e^{-m\tau}$ if $\tau \ll 1$, $e^{-m\tau} = (1 - m\tau)$ so $m = \alpha/(1 + \alpha\tau)$.

Now we shall introduce such a lag in development to maturity into the host-parasite model. Let

$\qquad\qquad$ τ_1 = maturation time for hosts

$\qquad\qquad$ τ_2 = maturation time for parasites

Assume only mature individuals can be hosts and that τ_1, τ_2 are small enough that terms of degree ≥ 2 in τ_1, τ_2 may be neglected. Then

$$\frac{dH}{dt} = \beta H(t - \tau_1) - \gamma_1 P(t) H(t)$$

$$\frac{dP}{dt} = -\delta P(t) + \gamma_2 P(t - \tau_2) H(t - \tau_2)$$

and, approximately,

$$H(t - \tau_i) = H(t) - \tau_i H'(t) \qquad i = 1, 2$$

$$P(t - \tau_2) = P(t) - \tau_2 P'(t)$$

Assume also that H and P are near H_0, P_0 so we may write $H(t) = H_0(1 + h)$, $P(t) = P_0(1 + p)$, h, p small. The D.F.'s become, approximately,

$$N_Q \frac{dh}{dt} = \beta \left[N_Q(1 + h) - \tau_1 N_Q \frac{dh}{dt} \right] - \gamma_1 N_Q P_0 (1 + h)(1 + p)$$

$$\frac{dh}{dt} = (1 + \beta\tau_1) = \beta(1 + h) - \gamma \frac{\beta}{\gamma} (1 + h + p)$$

$$\frac{dh}{dt} = - \beta\tau_1 \frac{dh}{dt} - \beta P$$

$$\frac{dh}{dt} = - \frac{\beta P}{1 + \beta\tau} \quad \text{(compare this with the result above } (m = \frac{\alpha}{1 + \alpha\tau}))$$

similarly

$$\frac{dP}{dt} = \delta h - \delta\tau_2 \left(\frac{dh}{dt} + \frac{dp}{dt} \right)$$

substituting the expression for dh/dt in the second equation,

$$\frac{dp}{dt} = \frac{\delta h}{1 + \delta\tau_2} + \frac{\delta\tau_2}{1 + \delta\tau_2} \cdot \frac{\beta}{1 + \delta\tau_1} p$$

$p = h = 0$ is an equilibrium point.

To determine stability of this equilibrium point, let p, h be small and consider the matrix of coefficients in the equations for dp/dt, dh/dt. It is

$$\begin{bmatrix} 0 & \dfrac{-\beta}{1 + \delta\tau_1} \\[3mm] \dfrac{\delta}{1 + \delta\tau_2} & \dfrac{\delta\tau_2}{1 + \delta\tau_2} \quad \dfrac{\beta}{1 + \delta\tau_1} \end{bmatrix}$$

The characteristic equation is:

$$\lambda^2 - \frac{\beta\delta\tau_2}{(1 + \beta\tau_1)(1 + \delta\tau_2)} + \frac{\beta\delta}{(1 + \beta\tau_1)(1 + \delta\tau_2)} = 0$$

If at least one of the roots has a positive real part then the solutions of the DE's will go to $+ \infty$ as $t \to + \infty$, i.e., the equilibrium will be unstable.

The sum of the roots $\lambda_1 + \lambda_2 = \dfrac{\beta\delta\tau_1}{(1 + \beta\tau_1)(1 + \delta\tau_2)} > 0$

$\therefore$ at least one of the roots has a positive real part. $\therefore$ the equilibrium is unstable.

Second Modification:

Ignore the lag in development to maturity, but assume that immigration occurs. Let

ϵ_1 = rate at which host population enters the region

ϵ_2 = rate at which parasite population enters the region

$$(\epsilon_1,\ \epsilon_2 \geq 0)$$

Then

$$\frac{dH}{dt} = (\beta - \gamma_1 P)\ H + \epsilon_1$$

$$\frac{dP}{dt} = (\gamma_2 H - \delta)P + \epsilon_2$$

Let $(P_0,\ H_0)$ be an equilibrium point. Then

$$(\beta - \gamma_1 P)\ H_0 + \epsilon_1 = 0\ ; \qquad\qquad (\gamma_2 H_0 - \delta)\ P_0 + \epsilon_2 = 0$$

or

$$\beta H - \gamma_1 H_0 P_0 + \epsilon_1 = 0\ ; \qquad\qquad -\delta P_0 + \gamma_2 H_0 P_0 + \epsilon_2 = 0$$

multiplying the first equation by γ_2; the second by γ_1, and adding:

$$2)\quad \beta\gamma_2 H_0 + \gamma_2 \epsilon_1 - \delta\gamma_1 P_0 + \gamma_1 \epsilon_2 = 0$$

since

$$H_0 = \frac{-\epsilon_1}{\beta - \gamma_1 P_0}$$

Upon substituting this into 2) we obtain

$$\delta\gamma_1 P_0^2 - P_0[\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta] + \beta\epsilon_2 = 0$$

so

$$P_0 = \frac{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta) \pm \sqrt{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta)^2 - 4\beta\gamma_1 \delta\epsilon_2}}{2\gamma_1 \delta}$$

The radical is equal to

$$\sqrt{(\gamma_1 \epsilon_2 + \beta\delta)^2 + (\gamma_2 \epsilon_1)^2 + 2(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1)\ \beta\delta - 4\beta\gamma_1 \delta\epsilon_2}$$

$$= \sqrt{(\gamma_1 \epsilon_2 - \beta\delta)^2 + (\gamma_2 \epsilon_1)^2 + 2(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1)\beta\delta}$$

so both roots are real. If

$$P_0 = \frac{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta) - \sqrt{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta)^2 - 4\beta\gamma_1\delta\epsilon_2}}{2\delta\gamma_1}$$

Then

$$H_0 = \frac{-\epsilon_1}{\beta - \gamma_1 P_0}$$

but

$$\beta - \gamma_1 P_0 = \beta - \frac{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta) - \sqrt{(\gamma_1 \epsilon + \gamma_2 \epsilon_1 + \beta\delta)^2 - 4\beta\delta\gamma_1\epsilon_2}}{2\delta}$$

$$= \frac{(\beta\delta - \gamma_1 \epsilon_2 - \gamma_2 \epsilon_1) - \sqrt{(\beta\delta - \gamma_1 \epsilon_2)^2 + (\gamma_2 \epsilon_1)^2 + 2\gamma_2 \epsilon_1 (\beta\delta + \gamma_1 \epsilon_2)^2}}{2\delta}$$

$$\leq \frac{1}{\delta}\left[(\beta\delta - \gamma_1 \epsilon_2 - \gamma_2 \epsilon_1) - \sqrt{(\beta\delta - \gamma_1 \epsilon_2)^2 + (\gamma_2 \epsilon_1)^2 + 2\gamma_2 \epsilon_1 (\beta\delta - \gamma_1 \epsilon_2)^2} \right]$$

$$= 0$$

so the smaller root gives $H_0 < 0$ and thus it must be rejected.

$$P_0 = \frac{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta) + \sqrt{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta)^2 - 4\beta\gamma_1\delta\epsilon_2}}{2\gamma_1\delta}$$

if ϵ_1, ϵ_2 are small enough that their squares may be neglected.

$$P_0 = \frac{(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta) + \sqrt{2\beta\delta(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1) + (\beta\delta)^2 - 4\beta\delta\epsilon_2\gamma_1}}{2\gamma_1\delta}$$

recalling $\sqrt{1 + x} \cong 1 + x/2$ if $0 \leq x \ll 1$

$$P_0 \cong \frac{1}{2\gamma_1\delta}\left[(\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 \beta\delta) + \beta\delta \sqrt{\frac{2\beta\delta(\gamma_2 \epsilon_1 - \gamma_1 \epsilon_2)}{\beta^2\delta^2} + 1} \right]$$

$$= \frac{1}{2\gamma_1 \delta} \left[\gamma_1 \epsilon_2 + \gamma_2 \epsilon_1 + \beta\delta + \beta\delta \left(1 + \frac{\gamma_2 \epsilon_1 \cdot \gamma_1 \epsilon_2}{\beta\delta} \right) \right]$$

$$= \frac{\beta}{\gamma_1} + \frac{\epsilon_1}{\delta} \frac{\gamma_2}{\gamma_1} = P_0$$

and

$$H_0 = \frac{\delta}{\gamma_2} - \frac{\epsilon_2}{\beta} \frac{\gamma_1}{\gamma_2}$$

To determine the nature of the equilibrium point (H_0, P_0), let

$$H = H_0(1 + h), \qquad P = P_0(1 + p) \qquad h, p \text{ small}$$

substituting into the D.E.'s

$$H_0 \frac{dh}{dt} = (\beta - \gamma_1 P_0(1 + p)) H_0(1 + h) - (\beta - \gamma_1 P_0) H_0$$

ignoring terms in p, h

$$\frac{dh}{dt} \cong -\gamma_1 P_0 p + h(\beta - \gamma_1 P_0)$$

and since

$$P_0 = \frac{\beta}{\gamma_1} + \frac{\epsilon_1}{\delta} \frac{\gamma_2}{\gamma_1}; \quad \frac{dh}{dt} = -\gamma_1 P_0 p - h\epsilon_1 \frac{\gamma_2}{\delta}$$

similarly,

$$\frac{dp}{dt} \cong \gamma_2 H_0 h - p\epsilon_2 \frac{\gamma_1}{\beta}$$

The matrix of the coefficients is:

$$\begin{bmatrix} -\epsilon_1 \frac{\gamma_2}{\delta} & -\gamma_1 P_0 \\ \\ \gamma_2 H_0 & -\epsilon_2 \frac{\gamma_1}{\beta} \end{bmatrix}$$

The characteristic equation is:

$$\lambda^2 + \lambda \left(\epsilon_1 \frac{\gamma_2}{\delta} + \epsilon_1 \frac{\gamma_1}{\beta} \right) + \gamma_1 \gamma_2 P_0 H_0 + \frac{\epsilon_1 \epsilon_2}{\beta\delta} \gamma_1 \gamma_2 = 0$$

$(\epsilon_1 \epsilon_2 \text{ may be ignored})$

Let λ_1, λ_2 be the two roots

$$\lambda_1 + \lambda_2 = -\epsilon_2 \frac{\gamma_2}{\delta} - \epsilon_1 \frac{\gamma_1}{\beta} < 0$$

$$\lambda_1 \lambda_2 = \gamma_1 \gamma_2 P_0 H_0 > 0$$

at least one must thus have negative real part. The other must either be real and negative (the product is positive, or it is the conjugate of the first). In either case, both have negative real parts. $\therefore$ h, p $\longrightarrow$ 0 $\therefore$ equilibrium is stable.

We shall now consider a model in which both a maturation lag and immigration is taken into account. Let ϵ_1, ϵ_2 be the immigration factor, as above, and let τ be the maturation time for both species. Assume ϵ_1, ϵ_2, τ are all small enough that their effects are additive, i.e., so that second order terms may be ignored.

The D.E.'s are:

$$\frac{dH}{dt} = \beta H(t - \tau) - \gamma_1 P(t) H(t) + \epsilon_1$$

$$\frac{dP}{dt} = -\delta P(t) + \gamma_2 P(t - \tau) H(t - \tau) + \epsilon_2$$

We saw earlier that the introduction of a lag to maturity did not affect the equilibrium points. Thus

$$H_0 = \frac{\delta}{\gamma_2} - \frac{\epsilon_2}{\beta} \frac{\gamma_1}{\gamma_2} ; \qquad P_0 = \frac{\beta}{\gamma_1} + \frac{\epsilon_1}{\delta} \frac{\gamma_2}{\gamma_1}$$

are the equilibrium points. Let $H(t) = H_0(1 + h(t))$, $P(t) = P_0(1 + p(t))$; p, h small. Recall that $H(t - \tau) \cong H(t) - \tau H'(t)$; $P(t - \tau) \cong P(t) - \tau P'(t)$.

$$\epsilon_1 = \gamma_1 P_0 H_0 - \beta H_0$$

$$\epsilon_2 = \delta P_0 - \gamma_2 H_0 P_0$$

Thus:

$$\not{H}_0 \frac{dh}{dt} = \beta \not{H}_0(1 + h - \tau h') - \gamma_1 P_0 \not{H}_0(1 + p + h) + \not{H}_0(\gamma_1 P_0 - \beta)$$

$$\frac{dh}{dt} (1 + \tau\beta) = h(\beta' - \gamma_1 P_0) + p(-\gamma_1 P_0) + (\beta - \not{\gamma_1 P_0}) + (\gamma_1 \not{P_0} - \beta)$$

$$\frac{dh}{dt} = h \left[\frac{-\epsilon_1 \gamma_2}{\delta(1+\tau\beta)} \right] + p \left[\frac{-\beta\delta - \epsilon_1\gamma_2}{(1 + \tau\beta)\delta} \right]$$

τ is small,

$$1 + \tau\beta = 1 - \tau\beta + 0(\tau\beta)^2 \cong 1 - \tau\beta$$

but we are assuming that $\tau\epsilon_1$, $\tau\epsilon_2 \ll 1$ so we can drop such terms

$$\frac{dh}{dt} \cong h \left[- \frac{\epsilon_1\gamma_2}{\delta} \right] + p \left[\frac{-\beta}{1 + \tau\beta} - \frac{\epsilon_1\gamma_2}{\delta} \right]$$

$$P_0 \frac{dp}{dt} = - \delta P_0(1 + p) + \gamma_2 P_0 H_0(1 + p(t-\tau) + h(t-\tau)) + P_0(\delta - \gamma_2 H_0)$$

$$\frac{dp}{dt} = - \delta(1 + p) + \gamma_2 H_0 [1 + p - \tau p' + h - \tau h'] + (\delta - \gamma_2 H_0)$$

$$\frac{dp}{dt} = (1 + p) [\gamma_2 H_0 - \delta] + (\delta - \gamma_2 H_0) + \gamma_2 H_0 h - \tau\gamma_2 H_0(p' + h')$$

$$\gamma_2 H_0 - \delta = - \frac{\epsilon_1\gamma_1}{\beta} \quad ; \quad \tau\gamma_2 H_0 \cong \tau\delta$$

$\therefore$
$$\frac{dp}{dt} (1 + \tau\delta) = p \left[\frac{-\epsilon_2\gamma_1}{\beta} \right] + \left(\delta - \frac{\epsilon_2\gamma_1}{\beta} \right) h$$

$$- \tau\delta \left[h \left(\frac{-\epsilon_1\gamma_2}{\delta} \right) \right] + \tau\delta p \left[\frac{\beta}{1 + \tau\beta} - \frac{\epsilon_1\gamma_2}{\delta} \right]$$

$$\frac{dp}{dt} (1 + \tau\delta) = h \left[\delta - \frac{\epsilon_1\gamma_1}{\beta} \right] + p \left[\frac{-\epsilon_2\gamma_1}{\beta} + \frac{\tau\delta\beta}{1 + \tau\beta} \right]$$

$$\frac{dp}{dt} = h \left[\frac{\delta}{1 + \tau\beta} - \frac{\epsilon_2\gamma_1}{\beta} \right] + p \left[\frac{-\epsilon_2\gamma_1}{\beta} + \tau\delta\beta \right]$$

The matrix of the coefficients is

$$\sum = \begin{bmatrix} \dfrac{-\epsilon_1\gamma_2}{\delta} & - \dfrac{\beta}{1 + \tau\beta} - \dfrac{\epsilon_1\gamma_2}{\delta} \\[2em] \dfrac{\delta}{1 + \tau\beta} - \dfrac{\epsilon_2\gamma_1}{\beta} & \dfrac{-\epsilon_2\gamma_1}{\beta} + \tau\delta\beta \end{bmatrix}$$

if λ_1, λ_2 are the eigenvalues,

$$\lambda_1 + \lambda_2 = \text{trace } \sum$$

$$\lambda_1 \lambda_2 = \det \sum$$

$$\lambda_1 + \lambda_2 = \frac{-\epsilon_1 \gamma_2}{\delta} - \frac{\epsilon_2 \gamma_1}{\beta} + \tau \delta \beta$$

$$\lambda_1 \lambda_2 = \frac{-\epsilon_1 \gamma_2}{\delta} \left[\frac{-\epsilon_2 \gamma_1}{\beta} + \tau \delta \beta \right] + \left[\frac{\beta}{1 + \tau \beta} + \frac{\epsilon_1 \gamma_2}{\delta} \right] \left[\frac{\delta}{1 + \tau \beta} - \frac{\epsilon_2 \gamma_1}{\beta} \right]$$

ignoring second order terms in τ, ϵ_1, ϵ_2

$$\lambda_1 \lambda_2 = \frac{\beta \delta}{(1 + \tau \beta)^2} - \epsilon_2 \gamma_1 + \epsilon_1 \gamma_2$$

since ϵ_1, ϵ_2 are small, λ_1, $\lambda_2 > 0$, so the equilibrium is stable if $\lambda_1 + \lambda_2$ is < 0, for then both roots must have negative real parts, since their product is positive.

Equilibrium is stable if $\dfrac{\epsilon_1 \gamma_2}{\delta} + \dfrac{\epsilon_2 \gamma_1}{\beta} > \tau \delta \beta$

$$H_0 = \frac{\delta}{\gamma_2} \left[1 - \frac{\epsilon_2 \gamma_1}{\beta \delta} \right] ; \qquad P_0 = \frac{\beta}{\gamma_1} \left[1 + \frac{\epsilon_1 \gamma_2}{\beta \delta} \right]$$

thus

$$\frac{\epsilon_1}{H_0} = \frac{\epsilon_1 \gamma_2}{\delta} ; \qquad \frac{\epsilon_2}{P_0} = \frac{\epsilon_2 \gamma_1}{\beta}$$

so the condition for stability becomes

$$\frac{\epsilon_1}{H_0} + \frac{\epsilon_2}{P_0} > \tau \beta \delta$$

II. General Competition Model

Consider two species, A and B. Let

$N(t)$ = size of A population at time t

$M(t)$ = size of B population at time t

α_1 = birth rate of members of A

α_2 = birth rate of members of B.

Then

$$\frac{dN}{dt} = \alpha_1 N(t) - F_1(N,M); \qquad \frac{dM}{dt} = \alpha_2 M(t) - F_2(N,M)$$

F_1, F_2 are some functionf of population size. For simplicity we shall assume they are of the form:

$$F_1(N,M) = (\beta_{11} N + \beta_{12} M) N \qquad\qquad B_{ij} \geq 0$$

$$F_2(N,M) = (\beta_{21} N + \beta_{22} M) M$$

so

$$\frac{dN}{dt} = N(\alpha_1 (\beta_{11} N + \beta_{12} M))$$

$$\frac{dM}{dt} = M(\alpha_2 (\beta_{21} N + \beta_{33} M))$$

the equilibrium is given by the solution to the equation $(\beta_{ij}) \binom{N}{M} = \binom{\alpha_1}{\alpha_2}$

Case 1. $\begin{vmatrix} \beta_{11} & \beta_{12} \\ \beta_{21} & \beta_{22} \end{vmatrix} = \Delta = 0$ so there is λ, $\beta_{12} = \lambda\beta_{11}$, let $\beta_i = \beta_{11}$.

Then

$$\frac{1}{N} \frac{dN}{dt} = \alpha_1 - \beta_1 (N + \lambda M)$$

$$\frac{1}{M} \frac{dM}{dt} = \alpha_2 - \beta_2 (N + \lambda M)$$

Note that if N, M are sufficiently large $\frac{dN}{dt}$, $\frac{dM}{dt} \leq 0$ so N, M are bounded.

We have $(\beta_2\, dN)/N - (\beta_1\, dM)/M = (\alpha_1\beta_2 - \beta_1\alpha_2)\, dt$

so

$$\beta_2 \log N - \beta_1 \log M = \begin{vmatrix} \alpha_1 & \alpha_2 \\ \beta_1 & \beta_2 \end{vmatrix} t + C$$

C is determined by the initial conditions.

$$\frac{N\beta_2}{M\beta_1} = Ke^{(\alpha_1\beta_2-\alpha_2\beta_1)t} \quad \text{if} \quad \begin{vmatrix} \alpha_1 & \alpha_2 \\ \beta_1 & \beta_2 \end{vmatrix} > 0$$

then as $t \to \infty$. $M(t) \to 0$ (species β dies out) if $\begin{vmatrix} \alpha_1 & \alpha_2 \\ \beta_1 & \beta_2 \end{vmatrix} < 0$,

$N(t) \to 0$ (A dies out); if

$$\begin{vmatrix} \alpha_1 & \alpha_2 \\ \beta_1 & \beta_2 \end{vmatrix} = 0, \text{ this model gives no information.}$$

Case 2. $\Delta \neq 0$

Then the equilibrium point (M_0, N_0) must be such that

$$\alpha_1 = \beta_{11} N_0 + \beta_{12} M_0$$

$$\alpha_2 = \beta_{21} N_0 + \beta_{22} M_0$$

$$N_0 = \frac{1}{\Delta} \begin{vmatrix} \alpha_1 & \beta_{12} \\ \alpha_2 & \beta_{22} \end{vmatrix} \quad ; \quad M_0 = \frac{1}{\Delta} \begin{vmatrix} \beta_{11} & \alpha_1 \\ \beta_{21} & \alpha_2 \end{vmatrix}$$

these must be > 0 for a positive equilibrium to exist.

Let

$$N(t) = N_0(1 + u), \quad M(t) = M_0(1 + v) \quad u, v \text{ small}$$

substituting these expressions into the D.E.'s

$$\frac{du}{dt} = -\beta_{11} N_0 u - \beta_{12} M_0 v; \quad \frac{dv}{dt} = -\beta_{21} N_0 u - \beta_{22} M_0 v$$

The matrix of coefficients is:

$$\begin{vmatrix} -\beta_{11} N_0 & -\beta_{12} M_0 \\ -\beta_{21} N_0 & -\beta_{22} M_0 \end{vmatrix}$$

the characteristic equation is

$$\lambda^2 + (\beta_{11} N_0 + \beta_{22} M_0) \lambda + M_0 M_0 \Delta = 0 ; \quad N_0, M_0, \beta_{11}, \beta_{22} > 0$$

∴ at least one char. root has negative real parts. If $\Delta > 0$, both have negative real parts, and (N_0, M_0) is a stable equilibrium. If $\Delta < 0$ both roots are real; one > 0, the other < 0. The equilibrium will be stable or not depending on the initial conditions.

III. Flowerbeetle Model

This material is the result of work by Park. There are two species of beetle,

<center>T-casteneum   T-confusum</center>

If both occur together in a region, only one will survive, but it is not always the same one. We may try to set up a deterministic model for this behavior.

Each beetle has 2 stages: active and passive; let

$P(t)$ = number of passive individuals at time t

$A(t)$ = number of active individuals at time t

μ = coefficient of voraciousness of active beetles

ν = rate of transition from passive to active

δ = density factor in the rate of growth

λ = growth rate of passive individuals, as offspring of active members at time 0.

ϵ = death rate (of active individuals)

$$\frac{dP}{dt} = -\mu A P - \nu P + (\lambda - \delta A)A \; ; \quad \frac{dA}{dt} = \nu P - \epsilon A$$

The equilibrium point is seen to be

$$P_0 = \frac{(\lambda - \epsilon)\epsilon}{\mu\epsilon + \nu\delta} \; ; \quad A_0 = \frac{(\lambda - \epsilon)\nu}{\mu\epsilon + \nu\delta} \quad\quad \text{if} \;\; \lambda \geq \epsilon$$

To determine the nature of the equilibrium, let

$$A = A_0(1 + a), \quad\quad P = P_0(1 + p) \quad\quad a, p \text{ small}$$

then

$$A_0 \frac{da}{dt} = \nu P_0(1 + p) - \epsilon A_0(1 + a)$$

$$\nu \frac{da}{dt} = \nu\epsilon(1 + p) - \nu\epsilon(1 + a)$$

$$\frac{da}{dt} = -\epsilon a + \epsilon p$$

$$P_0 \frac{dp}{dt} = -\mu A_0 P_0 (1 + a + p) - \nu P_0 (1 + p) + (\lambda - \delta A_0(1+a)) A_0(1+a)$$

after algebraic manipulations, the constant terms cancel and we obtain

$$\frac{dp}{dt} = a \left[\frac{\mu\nu\epsilon^2 - \nu^2\lambda\delta + 2\delta\epsilon\nu^2}{\epsilon(\mu\epsilon + \nu\delta)} \right] + p \left[\frac{-\mu\nu\lambda - \nu^2\delta}{(\mu\epsilon + \nu\delta)} \right]$$

The matrix of the coefficients is

$$\sum = \begin{bmatrix} -\epsilon & \epsilon \\ \dfrac{\mu\nu\epsilon^2 - \nu^2\lambda\delta + 2\delta\epsilon\nu^2}{\epsilon(\mu\epsilon + \nu\delta)} & \dfrac{-\mu\nu\lambda - \nu^2\delta}{(\mu\epsilon + \nu\delta)} \end{bmatrix}$$

let λ_1, λ_2 be the eigenvalues. Then

$$\lambda_1 + \lambda_2 = \text{trace} \sum ; \qquad \lambda_1 \lambda_2 = \det \sum$$

$$\lambda_1 + \lambda_2 = -\epsilon - \frac{\mu\nu\lambda - \nu^2\delta}{(\mu\epsilon + \nu\delta)} < 0$$

$$\lambda_1\lambda_2 = \frac{\epsilon(\mu\nu\lambda - \nu^2\delta) - (\mu\nu\epsilon^2 - \nu^2\lambda\delta)}{(\mu\epsilon + \nu\delta)} = \nu(\lambda - \epsilon)$$

If $\lambda > \epsilon$, $\lambda_1\lambda_2 > 0$; since at least one of the roots is negative, this means they both are negative, and equilibrium is stable. If $\lambda < \epsilon$ then the only equilibrium point is $P_0 = A_0 = 0$; since $\lambda_1\lambda_2 < 0$ in that case, the equilibrium may be unstable.

If $\lambda = \epsilon$, then $P_0 = A_0 = 0$ is the only equilibrium point, and it may be stable, unstable, or oscillatory, depending upon the initial conditions.